XXVIII.—*On the Germination of the Resting Spores, and on a form of Moving Spores in* Spirogyra. By Dr. W. Pringsheim*.

[Concluded from p. 218.]

[With two Plates.]

I now pass to the account of those structures which I have found in the spores, and certain others met with in the filament-cells of *Spirogyræ*, and of which I presuppose that they likewise serve for the reproduction of the *Spirogyræ*. The same, or some phænomena similar to those I have detected, probably led Agardh to the idea that the large spores became broken up into zoospores†.

I have little to add to what has been stated at page 211 concerning the secondary cells originating in the spores from their contents. The transformation of the contents of the spores into these cells is by no means rare. They present either the appearance shown in fig. 7, of little round cells with granular contents, or, as Meyen‡ represented them, of similar cells, but with contents consisting only of *one single homogeneous* grain, almost entirely filling the cell. I have not been able to detect movement or germination in them.

The structures existing in the filament-cells are more interesting. I frequently found, namely, in conjugated filaments, that the contents of one or more pairs of conjugated cells were not transformed into the well-known large spore. But while in unconjugated cells, in which no spore was produced, the contents became decomposed, exhibiting a disappearance of chlorophyll and simultaneous appearance of a red-brown colouring matter, in perfectly indefinite although here and there granular forms (Pl. VIII. fig. 1 *o*), the contents of *such conjugated* filament-cells as produced no solitary spore, became transformed into a number of little cells of regular, definite and unchangeable form (Pl. VIII. fig. 4). This regular occurrence led me to conjecture that these cells were more than mere pseudo-forms of decaying cell-contents. I first obtained an insight into these structures by observation of their production in the cells of the young *Spirogyræ*, which I had myself seen emerge from large spores. In the cells of *these young Spirogyræ* the existing spiral bands are often broken up, and from their substance are formed, in a manner still unknown to me, little cells in which a membrane can be

* From the 'Flora,' Aug. 14th and 21st, 1852: translated by Arthur Henfrey, F.R.S., F.L.S.

† Vide p. 211, note ‖.

‡ Pflanzenphysiologie, iii. pl. 10. fig. 13 *c*, *d*, *e*.

clearly detected surrounding green contents (Pl. IX. fig. 8 *a*). I call these cells spore-mother-cells. They soon increase in size, their membrane separating itself from the contents, and expanding into a largeish hollow vesicle. The contents at the same time acquire a yellowish or yellow-brown colour, and separate into a *central*, denser, yellow-brown nucleus, and a finely granular mucilage, which surrounds the nucleus and does not entirely fill the space between it and the membrane (Pl. IX. fig. 8 *b*, *c*, *d*, *e*). This finely granular mucilage then becomes balled together, in the space between the yellow nucleus and the surrounding membrane, into a single large corpuscle exhibiting a sharply defined outline, and appearing as a transparent vesicle with finely granular contents (fig. 8 *f*, *f*). The new cell thus formed pushes the brown body, as the figures show, out of its central position, against the wall of the parent-cell or the spore-mother-cell. The pressure of these two bodies causes the rupture of the membrane of the spore-mother-cell; the *transparent* cell emerges and moves about independently and freely in the filament-cell in the manner of the zoospores.

The expelled zoospores are small elliptical cells; seen from the side they appear longish (fig. 8 *g*), from above, round (fig. 8 *h*). Their aspect resembles that of the moving spores of *Achlya prolifera* more than of any others. Their movement is much slower than that of other zoospores, and is further distinguished by the fact, that in advancing they do not make a *complete* revolution round their longitudinal axis, but merely slight oscillations to the right and left. In moving about they traverse the cavity of the filament-cells in all directions, mostly gliding onwards along the wall, as if, as it were, seeking an orifice whereby to escape; but notwithstanding that I observed very many of these moving cells for long-continued periods, I never saw them emerge from the filament-cells in which they had been produced, since no orifice was ever formed in the *everywhere closed* filament-cells. That these cells possess locomotion-threads (cilia) is certain; I could often detect them *in vibration* with the greatest clearness; but as I remained in uncertainty as to the number of vibrating threads, I have omitted them altogether in the drawing. I think it most probable that they have one single thread at the anterior extremity; yet in certain cases it appeared as if they bore a crown of several threads.

After wandering about unceasingly for several hours, they finally fix themselves *by the point*. All, however, that I have observed, after they had come to rest, became decomposed without further organic development, and their contents, *which, so long as they were in motion, were always coloured yellow and never blue with iodine*, became transformed into a number of very

small, irregular starch-granules, coloured blue by iodine (Pl. IX. fig. 8 *i*, *i*), around which could often be detected an enveloping coat, the membrane of the dead spore. The spore-mother-cell from which the moving spore has escaped (fig. 8 *k*, *k*, *l*), only changes so far that the yellow-brown nucleus lying in it acquires a regular outline and an indistinct structure. *The orifice through which the moving spore has escaped, may still always be distinguished in the membrane of the mother-cell, if its position is not too unfavourable* (fig. 8 *k*, *k*, *l*, *l*). The spore-mother-cells exactly resemble those structures which I had found in the *conjugated* cells of old filaments (Pl. VIII. fig. 4*).

I have met with the following inessential variations from ordinary course of formation of the moving spores in the spore-mother-cells just described. Frequently several moving spores are formed, instead of one, in a spore-mother-cell, and this is the cause of the variable size of the spores. Moreover, one or more little brown corpuscles—portions of the central brown-yellow nucleus of the spore-mother-cell—are often combined with the finely granular mucilage which collects in the spore-mother-cell for the formation of the spores. In such cases the free spore likewise possesses one or more brown-yellow nuclei. Finally, the finely granular mucilage inside the spore-mother-cell frequently never arrives at the formation of the spore, but is transformed at once into starch-granules (Pl. IX. fig. 8 *m*).

The question now arising, how we are to interpret these moving structures, it appears to me that their *mode of formation* and the *regularity* of their appearance necessarily repel the idea that they are accidental, abnormal productions, without further value in the development of the plant. That they are foreign structures, not belonging to the *Spirogyræ*, would be an altogether inadmissible hypothesis, *since they are formed in the interior of the closed filament-cells of the* Spirogyræ, *directly from their contents*; for how, supposing them to be Infusoria, should an earlier generation of them have come into a closed cell? or is it probable that such Infusoria, produced by a *generatio æquivoca*, would begin and end their life in the interior of a vegetable cell?

In my opinion the most direct and simplest assumption, in the present condition of science, is, that they are propagative cells of the *Spirogyræ*, capable of development, and if set free, under favourable circumstances, from the filament-cell during their motion, they would reproduce the parent plant.

* When I drew fig. 4, I was still unacquainted with the history of development of this cell, and overlooked the orifices in the outer membrane through which the moving spore had emerged. Subsequently, however, *I could in every case see these orifices most distinctly in these cells, also, occurring in the conjugated cells of old filaments.*

According to this hypothesis, the contents of the filament-cells of the *Spirogyræ* might form, sometimes a large immediately-germinating, single spore (fig. 1 *a*, *b*, *c*, fig. 5), sometimes several parent-cells of moving spores (figs. 4, 8), and the contents of already formed single spores might, instead of germinating immediately, undergo metamorphosis into a number of propagative cells equally capable of propagation (compare fig. 7. Pl. VIII. and Agardh's statement, page 211; Agardh having probably seen the contents of the *spores* converted into the same moving cellules which I found in the contents of the *filament-cells*). This apparently strange behaviour finds however its explanation, in the fact that the Algæ in general, as may be shown by reference to similar phænomena, are possessed of a greater variety of *forms of spores* than was formerly supposed. And that the form of the propagative cell may vary between wider limits in these simple plants, does not appear remarkable, when we reflect that the independence of the life of the individual cell is, of all plants, greatest among the Algæ, and that the capability of bringing forth the same species is in them alone peculiar to the *contents* of the individual vegetative cell. Why should this preserve only in one, and not in more, persistent or transitory resting forms, the reproductive power dwelling in it? Can nature have here connected the maintenance of the species with one single form, where she yet has committed the power of reproduction profusely to the *mass of contents of each individual* vegetative cell?

The very occurrence simultaneously of moving and motionless spores in the same plant is but an expression of this possibility of *variation of form* of the spores of the same species. For it is untenable to attribute to the moving form a value different from the motionless, and to call the moving germs, say propagative gonidia, and the motionless true spores, since both correspond in the same way to the universal law of formation of seed in true asexual plants, *to form reproductive cells by the immediate metamorphosis of the contents of the vegetative cells.* But the capacity of reproduction in the contents of the vegetative cells is not connected merely with one *single* form of moving and one *single* form of motionless spore, and in this especially is most distinctly shown the great independence of the contents of the individual cells of the lower plants. It is true that the contents of the spore-mother-cells constantly assume a form of moving or motionless spore determinate for each species in the *ordinary* course of the cell's life, and thence we see one propagate almost exclusively by *one* definite form of moving spore, another almost exclusively by *one* definite form of motionless spore; but when the *formation of this ordinary, normal form,* or the *development of their already complete normal form* is prevented, the contents of the spore-

mother-cells, or the contents of the already formed spore, give origin to these other, rarer forms, in which the capability of reproduction is likewise either permanently or transitorily secured to the cell-contents.

Examples of manifold forms of spores in the same species have indeed often presented themselves to observers, but hitherto have been mostly regarded as abnormal cell-formations, and no further estimated. In spite of the slight attention directed to these structures, many undoubted phænomena referable here may already be indicated, of which, however, I shall only cite a few.

The contents of the individual cells appear to be capable of producing new individuals in other ways than by the forms of spores already mentioned, in the *Spirogyræ*. Vaucher*, namely, whose observations may be regarded as correct, even when not yet extensively confirmed, saw the contents of isolated cells of his *Conjugata anyulata* (*Mougeotia genuflexa*) transformed directly into a young plant, without having first assumed a definite resting form, and emerge from the cell, as it were born alive; and Dillwyn†, on the other hand, observed that *this* plant formed seed in the same way as the rest of the Zygnemaceæ. The observation also on the division into four of the spores of *Mesocarpus scalaris*, made by Thwaites and published by Montagne‡, is to be included here, like so many other observations of the division of spores. But such a division of spores into *many* daughter-spores, does not afford any distinctive character of species or genera; it is possible in all propagative cells of a great number

* *Loc. cit.* p. 80. pl. 8. figs. 7, 8, 9. Here, the cell which grows into a new *Spirogyra*, and which ordinarily, in the normal spores of the Zygnemaceæ, is formed subsequently on the inside of two membranes thrown off in the germination, appears to have been formed directly in the cell of the parent plant, without these coats.

† British Confervæ, London, 1809, p. 18. The passage runs:—"I have since discovered the seeds of *Conferva genuflexa*; they are large and globular, and not found within either filament as in *Conferva jugalis* (*Spirogyra jugalis*), but in the connecting tube, which thereby becomes greatly distended, as it is represented in my supplementary plate. *M. Vaucher could not discover the seeds of this species*, and of the nature of his observations I cannot form any conjecture." The figure of *Conferva genuflexa* cited by Dillwyn, as well as the reference to the passage in Vaucher, leave no room for doubt that it was the *Mougeotia genuflexa* on which Dillwyn made his observations, and that Vaucher and Dillwyn investigated the same plant. I will remark in passing, that, consequently, the seeds of *Mougeotia* are not only known, but also represented by Dillwyn (*op. cit.* Supp. pl. C), and then the distinction between the genera *Mougeotia* and *Mesocarpus* founded on the want of spores in the former falls away.

‡ Duchartre, 'Revue Botanique,' 1846, p. 469, or the Report on this notice in Mohl and Schlechtendahl's 'Botanische Zeitung,' 1846, p. 498. The Report agrees exactly with the text of the notice.

of Algæ and organisms allied to them, the limits of its extension being at present indeterminable.

I have made an observation similar to that on the origin of moving spores in the cells of the young *Spirogyræ* (Pl. IX. fig. 8) in the spores of *Œdogonium tumidulum*, after they had already come to rest and had formed a radical prolongation at one end, as in the commencement of germination. Thuret*, in his splendid illustrations of the moving spores of Algæ, has figured two locomotive, but already resting spores of *Œdogonium vesicatum* (Link, not Kützing), from the summits of which the membrane has separated all round, like a lid, by a transverse slit, and he remarks that the green contents of such spores had always vanished. I had an opportunity of repeating this observation (fig. 12 *e*), but found that the contents of such spores, before vanishing out of the upper orifice, had become metamorphosed into a number of little *moving* spores, exactly resembling those which I had found in *Spirogyra jugalis* (fig. 12 *b*, *c*). I could not trace completely the transformation of the green contents of these spores into the moving cells; but the appearance of similar large cells with brown nuclei and lighter contents separate from the nucleus, before the formation of the moving cells (fig. 12 *d*, *d*), exactly as in *Spirogyra jugalis*, led me to conjecture that their formation takes place in the same way as in that case.

The moving cells exactly resemble those of *Spirogyra jugalis* in shape, size, and motion. I have not, indeed, observed their exit from the spore which comes to rest, myself, but have frequently found the empty spore with the detached lid; the place, also, where the lid is to separate subsequently is very frequently indicated beforehand, and I often saw the lid already *separated all round*, but not yet removed (fig. 12 *a*, *d*), while the transformation of the contents of the spore into moving cells was yet incomplete. If, as is probable, the clear cellules of *Œdogonium* are capable of propagating, these plants also may present, besides the resting form of spore which is produced in the enlarged cells, and whose germination is equally unknown at present, and the ordinary moving form of spore, a third equally mobile form of spore.

Of analogous occurrences in plants of other families, I will further refer to those observations which I have made on *Achlya prolifera*†, standing so nearly allied to the Algæ in its physiological phænomena, because these leave no doubt as to the *power of germination* of the *daughter-spores* produced in the *spores*

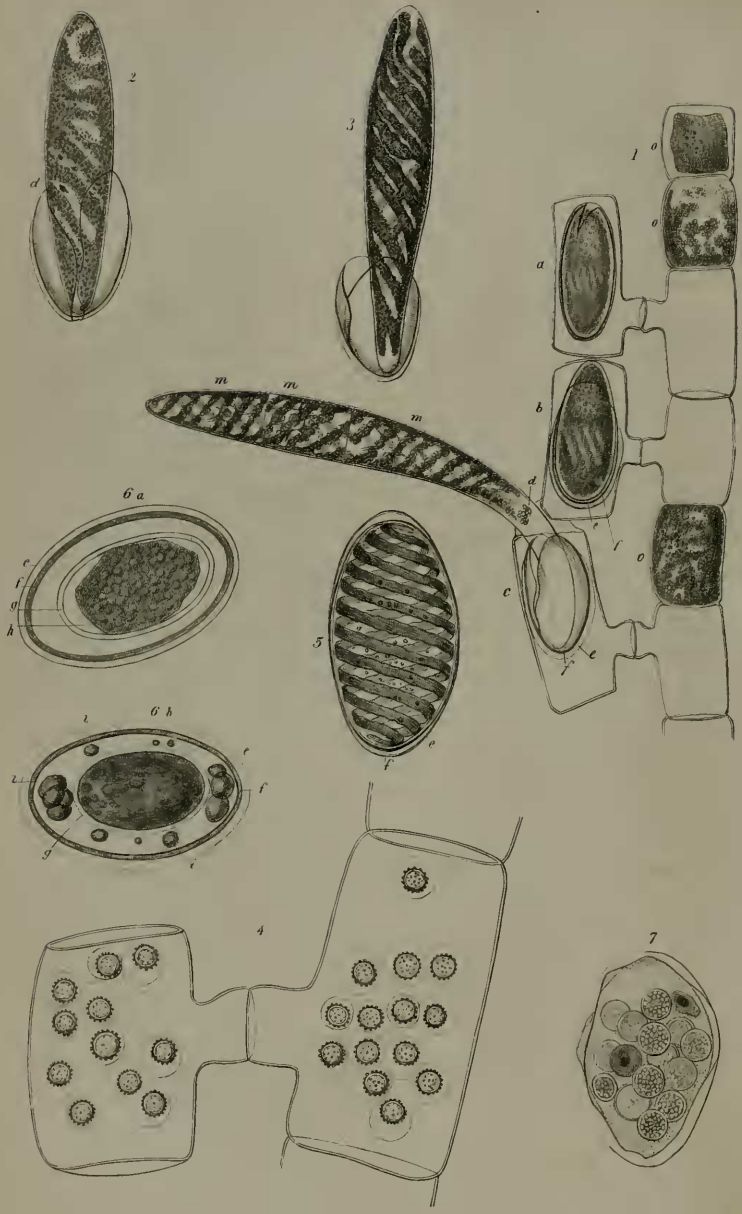
* Ann. des Sc. Nat. 1850, Sér. 3. xiv. 26. tab. 14. fig. 9.

† Die Entwickl. der *Achlya prolifera*, Nov. Acta A. N. C. xxiii. pars 1. 397.

capable of direct germination, while the third form of spore in *Achlya* reminds one in the most striking manner of the above-described moving spores of the *Spirogyræ*. Here again are formed inside the mother-cells of the resting spores, in rare cases, instead of the ordinary large globular spores, smaller (likewise resting ?) spores of a form more resembling the well-known moving spores of *Achlya* (Pl. IX. fig. 13); or these same smaller spores are formed, after the complete development of the ordinary resting spores, *in the individual resting spores themselves and from their contents.* I was able to observe directly the germination of these daughter-spores in *Achlya*. Here, therefore, there certainly exist three different forms of spores capable of germination, one of which originates, as in *Spirogyra,* by cell-formation in the contents of a form of spore likewise capable of germination *.

These circumstances lead me to consider as certain the possibility of the formation of various forms of spore in the same plant, and out of the *same contents destined for reproduction.* I have already mentioned, at the outset, that in each species, *one,* as it were normal form, is distinguished, among the various *possible* forms of spore, by the preponderating frequency of its occurrence, from the other rarer and generally exceptionally produced forms. But that those rarer, or if it be wished, abnormal forms, are nevertheless quite as capable of reproducing the parent plant, as the so-called normal form, appears to me quite beyond doubt, and for some, *e. g.* in *Achlya,* directly demonstrable. That the formation of the abnormal forms is subject to as definite morphological laws, as the formation of the normal form, follows from the regularity of the mode of their formation and the constancy of their appearance. It moreover seems to me probable, that the above-described production of moving, colourless spores, in large mother-cells possessing a brown nucleus, is not limited merely to *Spirogyra* and *Œdogonium,* but perhaps represents a very general type of formation of, in my sense abnormal—*i. e.* rare, merely appearing under exceptional conditions of vegetation—forms of spore. I shall only add here, that I have found exactly the same cells with detached coats and a brown nucleus, somewhat as in *e,* fig. 8. Pl. IX., in apparently dead cells in *Cladophora fracta* also, and the exactly similar figured in *f,* fig. 8, in decaying, still closed cells of young plants of *Nitella syncarpa.*

* I also observed in *Achlya* a division of the moving cells (figs. 14 *a*, *b*, *c*, *d*, *e*); these often become constricted in the middle (fig. 14 *b*) instead of germinating, after they have come to rest, and the two halves separate from each other until perfectly (fig. 14 *c*, *d*, *e*) distinct, each then acquiring a locomotive thread (cilia) and moving freely, like the mother-spore.



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